

TATARIAN PALYNOLOGY OF THE RUSSIAN PLATFORM: A REVIEW

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The Tatarian Stage of the Upper Permian succession on the Russian Platform has special significance in the history of stratigraphy. In particular the section exposed along the valley of the Vyatka River, which forms the effective stratotype of the Permian System as it was originally conceived by Murchison. Tatarian sediments are widely distributed on the Platform and have a total thickness of approximately 500 m. They represent a complex of deltaic plain, fluvial and lacustrine deposits, and have been separated into three horizons: the Urzhumskian at the base forms the lower Tatarian, and in ascending order, the Severodvinskian and Vyatskian make up the upper Tatarian.

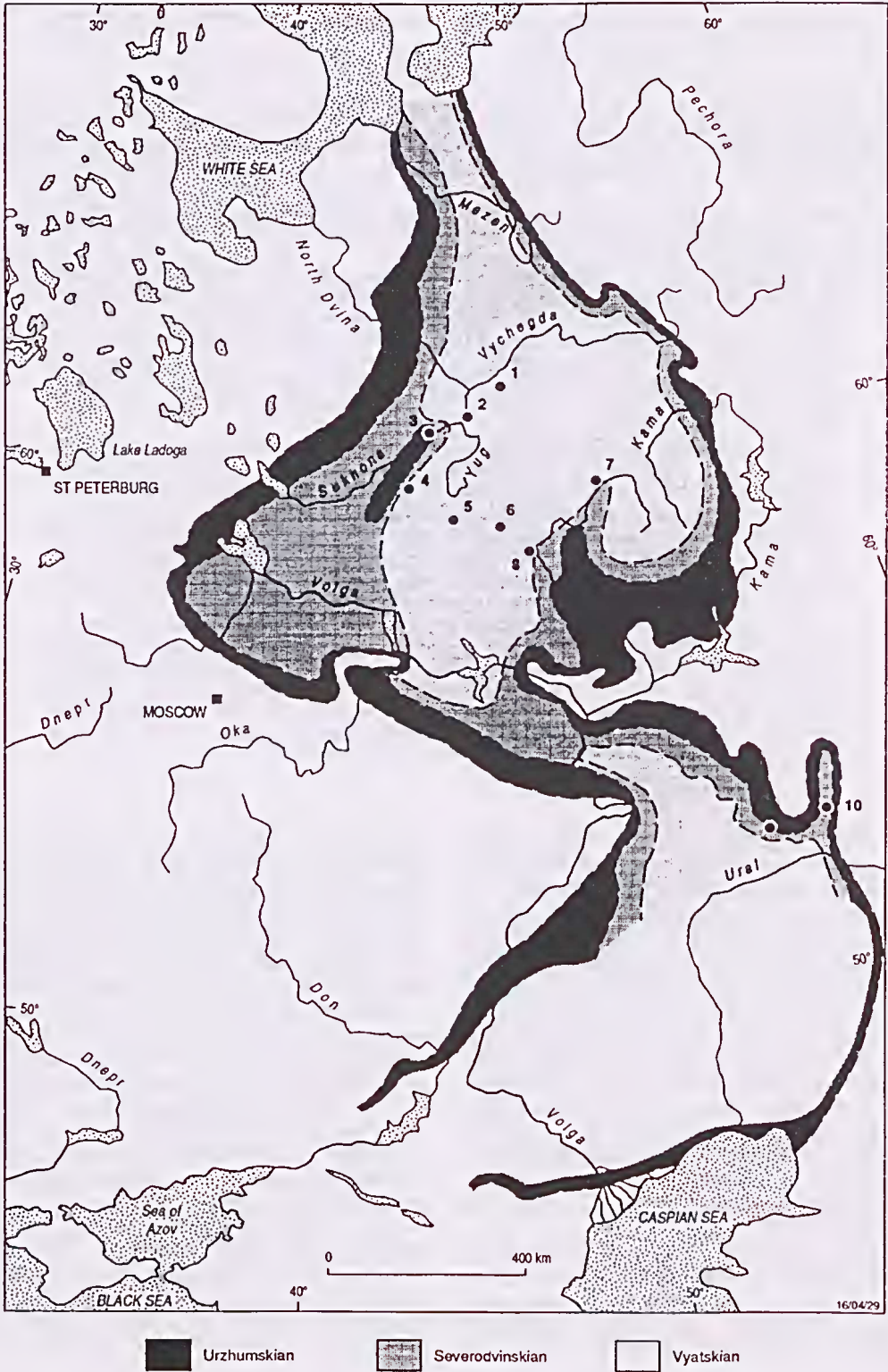
Plant microfossils are particularly important in correlating these deposits, and many Russian studies have been completed over the past 44 years, following the pioneering study of Zoricheva & Sedova in 1954. Many of these studies, however, are not readily accessed by those unfamiliar with the Russian language. Moreover, despite the considerable volume of work, no comprehensive palynostratigraphic synthesis yet exists. Earlier studies were concerned with taxonomy of the fossil spores and pollen, with little attention to their stratigraphic distribution; although it was recognised that the Tatarian assemblages had much in common with those from the underlying Kazanian, but differed sharply from those from the Lower Triassic Vettulian Formation.

In this paper we discuss: the composition of the Tatarian palynofloras, noting that disaccate pollen are the principal elements; their natural affinities; and their stratigraphic succession. Four palynological assemblages, designated informally as zones I to IV, are recognised, and key taxa are illustrated. Selected comparisons with Late Permian palynofloral assemblages from elsewhere in Europe and the Salt Range completes the review. The appearance of Tatarian pollen in Gondwanan and Cathaysian Permian deposits raises the question of parallelism to explain their presence; and research to address this is continuing.

THE TATARIAN Stage of the Upper Permian succession on the Russian Platform has special significance in the history of stratigraphy. In particular the section exposed along the valley of the Vyatka River, forms the effective stratotype of the Permian System as it was originally conceived by Murchison. Although designated as a Stage, the type Tatarian is effectively lithostratigraphically defined, as is any reference section for any other Stage, and because of its contained endemic faunas, and other non-marine fossils, it has been regarded as difficult to define in biostratigraphic terms. Three horizons (in Russian usage) are now generally recognised within the Tatarian: the Urzhumskian at the base forms the lower Tatarian, and in ascending order, the Severodvinskian and Vyatskian make up the upper Tatarian.

Tatarian sediments are widely distributed on the Russian Platform (Fig. 1) and have a total thickness of about 500 m. The sequence consists mainly of continental redbeds, but displays considerable lithological heterogeneity. Its stratigraphy and the

significance of its facies variability, in terms of depositional environment, have been described and discussed in considerable detail by Ignatiev (1962, 1963, 1987) who regarded the generally regressive sequence as a complex of deltaic plain, fluvial and lacustrine deposits (see also Gorbatkina & Stok 1984; Stok 1987; Tsvetkov 1987). As a result the fossil invertebrate, vertebrate and macroscopic plant remains represent organisms adapted to these specialised environments and have proved difficult to use for inter-regional correlation. For this reason palynology assumes particular importance for biostratigraphic purposes, as spores and pollen are plant entities that are less subject to phenotypic responses than plant foliage and axes. Palynomorphs are abundant and diverse in Tatarian sediments and have been the subject of many publications since the pioneer study of Zoricheva & Sedova (1954). Many subsequent accounts (e.g. Plotnikov 1964; Kyuntzel 1965; Sivertseva 1966b; Plotnikov & Molin 1969; Molin & Muravyova 1970; Molin & Koloda 1972; Varyuchina et al.



1981) have dealt with assemblages from various localities on the Russian Platform, but principally from the northern Severnaya Dvina and Mezen Basins. Another important stratigraphical contribution is that of Kyuntzel, based on studies of Tatarian and Lower Triassic material from the Upper Volga region, carried out more than 25 years ago, but only widely available more recently (Kyuntzel in Gomankov et al. 1986).

All the above papers are in Russian and many of their details are therefore not readily accessible to those unfamiliar with the language. In an attempt to overcome this, the present paper summarises, illustrates and critically interprets some of the data available, so that they may be more widely disseminated and assessed by workers in other countries. The account is necessarily brief and its conclusions are not fully argued, but a comprehensive monograph is in preparation by the senior author.

SAMPLING LOCALITIES

Tatarian palynological data are based on assemblages recovered from sediments encountered in drillholes or sampled in outcrop. Brief details of sources mentioned in the text or plate captions are set out in Table 1 and their localities indicated on Fig. 1.

DEVELOPMENT OF RUSSIAN TATARIAN PALYNOLOGY

Despite the now considerable volume of published work on the Tatarian no comprehensive palynostratigraphic synthesis yet exists. Early workers were principally concerned with the description of spores and pollen from isolated localities and paid little attention to their stratigraphic distribution, although they recognised that Tatarian assemblages

Locality	Description	Horizon
Alexandrovka	Left bank of the Kuplya River, 100 m downstream of the bridge at v. Novo-Alexandrovka (Orenburg district)	Severodvinskian
Aristovo	Right bank of the Malaya Severnaya Dvina River, 100 m upstream of the Aristovo landing place	Vyatskian
Kalinovka	Borehole #361, drilled in v. Kalinovka (Kostroma district), depth 153.6–160.0 m	Vyatskian
Kitchkas	Right bank of the Bolshoi Uran River, 1.5 km north-west of the bridge at v. Kitchkas (Orenburg district) at the mouth of an abandoned mine	Urzhumskian
Kotelnich	Right bank of the Vyatka River, 13 km downstream of the town of Kotelnich (Kirov district)	Severodvinskian
Lputyug	Borehole #529, drilled in v. Lputyug (Kirov district), depth 108.1–113.7 m	Vyatskian
Mulino	Right bank of the Vyatka River near v. Mulino (Kirov district)	Vyatskian
Titovo	Borehole #4, drilled 1.5 km north of v. Titovo (Vologda district), depth 138.0–144.4 m	Vyatskian
Viled	Borehole #6, drilled in v. Pavlovskoye, near the bridge over the Viled River (Arkhangelsk district), 139.0–154.5 m	Vyatskian
Vostroye	Left bank of the Sukhona River, opposite v. Vostroye (Vologda district)	Urzhumskian

Table 1. Summary of localities mentioned in text and figure captions.

Fig. 1. Geographic distribution of the Urzhumskian, Severodvinskian and Vyatskian Horizons of the Tatarian Stage on the Russian Platform. Sample localities (numbered): 1, Viled; 2, Aristovo; 3, Vostroye; 4, Titovo; 5, Kalinovka; 6, Lputyug; 7, Mulino; 8, Kotelnich; 9, Kitchkas; 10, Alexandrovka (see Table 1).

had much in common with those of the Kazanian and differed sharply from those of the overlying Lower Triassic Vetlugian Formation. In addition, despite their morphographic emphasis, most of the older papers cannot be used with confidence today, as they provide neither detailed descriptions nor adequate illustrations of the plant microfossils recognised.

A further difficulty is that, until relatively recently, no stable palynological systematic procedures have been accepted generally in Russia. Prior to about 1970 it was general practice to refer many dispersed palynomorph species to plant macrofossil, or even extant, genera. Thus disaccate pollen was referred to conifers or *Caytonia*, and monosulcate grains to 'ginkgocycadophytes' although Zauer (1960a) recognised that taeniate disaccate pollen derived from extinct plant groups, and attributed it to 'pteridosperms'. Current opinion is that the assemblages studied by Zauer are of Kazanian rather than Tatarian age.

These systematic practices gave rise to misleading nomenclature and resulted in the proliferation of taxa with imprecise diagnoses, which could not be used by later Russian, let alone foreign, workers. Dubious or erroneous assignments were also, at times, used as a basis for highly speculative palaeofloristic reconstructions (e.g. Zoricheva & Sedova 1954; Sivertseva 1966a) which, not unexpectedly, do not survive critical appraisal. An exception may be the discussion by Zauer et al. (1969) who analysed Late Permian assemblages from the Russian Platform in relation to those from coeval strata in Siberia and India and concluded that the three regions were phyto-geographically distinct at that time. Meyen (1973, 1979) subsequently supported this view, arguing that obvious and pronounced morphographic similarities between many of the palynomorph taxa from the three regions were the result of widespread parallelism, in plant groups that were not closely related (see further discussion below).

Palynological contributions that are relevant to Tatarian studies, although they relate to other stages of the Permian or to different palaeo-phytogeographical provinces, include the papers of

Samoilovich (1953), Sedova (1956) and Zauer (1960b), as well as the monographs of Luber & Waltz (1941), Andreyeva et al. (1956), and Varyukhina (1971). More recently three monographs have appeared (Virbitskas 1983; Tuzhikova 1985; Yaroshenko et al. 1991) that provide adequate descriptions of several species that are widespread in the Tatarian Stage, but again they deal with areas remote from the Russian Platform.

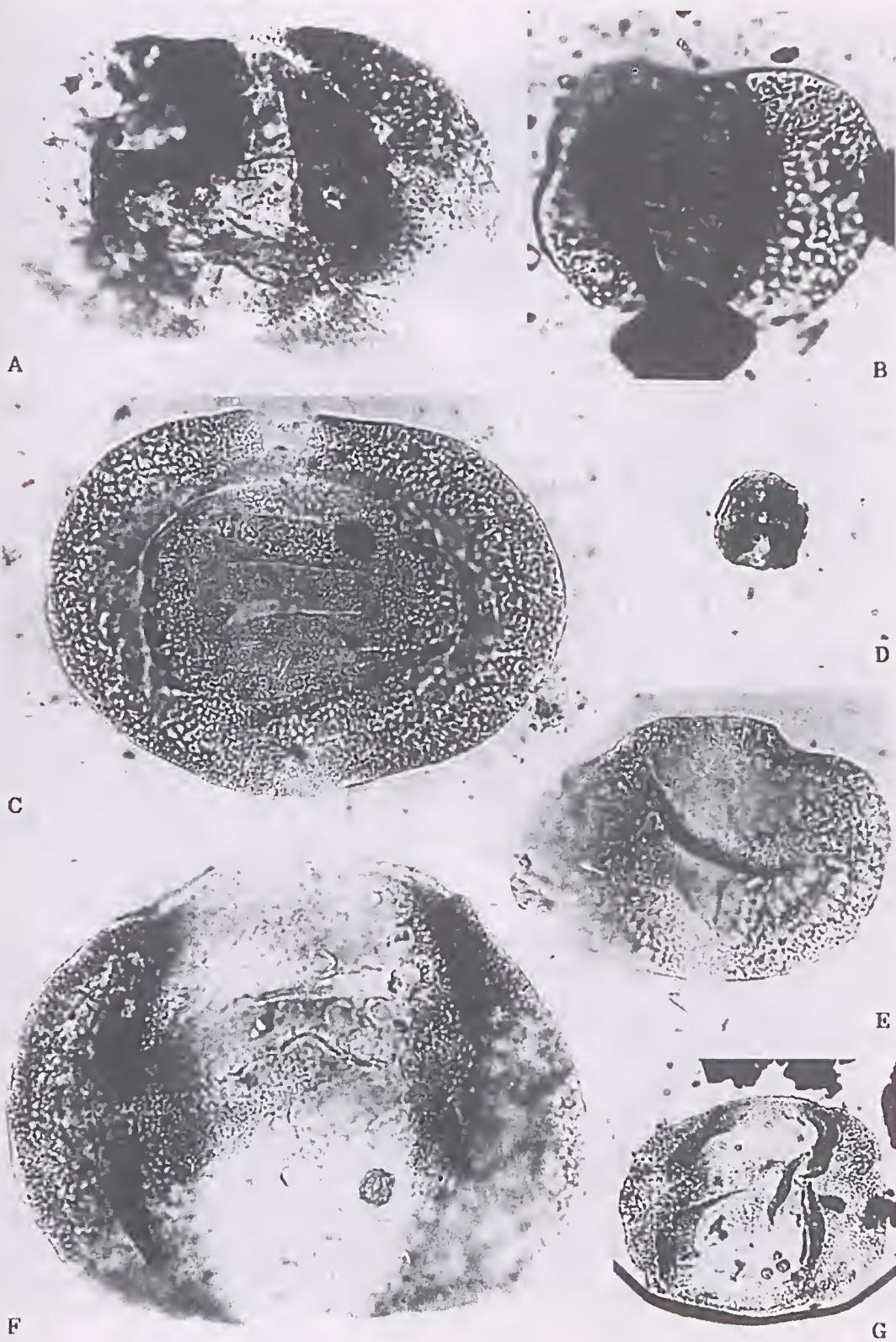
The systematics and stratigraphic distribution of pollen grains of the *Vittatina*-complex, which are so characteristic of Permian deposits of the Russian Platform, have been documented to a certain extent by Dyupina (1975), Stanitchnikova (1980) and Koloda (1986b, 1989) but more detailed treatment is still necessary. Also, the classification of taeniate pollen proposed by Efremova (1966) has been widely adopted, but the names of the new genera that she proposed are junior synonyms.

COMPOSITION OF TATARIAN PALYNOFLORAS

General

Disaccate pollen grains are the principal elements of Tatarian assemblages from the Russian Platform. Undoubtedly eusaccate pollen (*sensu* Foster 1979) are rare in the Late Palaeozoic and all the saccate Tatarian genera appear to be protosaccate (as defined by Scheuring 1974) or quasisaccate (in the sense of Meyen 1987), although in compressed specimens it is admittedly difficult to be completely sure of the saccus infrastructure without TEM data. Most of these disaccate forms have a cappa on which the exoexine is divided by clefts into longitudinal bands. Russian workers recognise two groups within pollen displaying such a structure. Genera such as *Lunatisporites*, in which the exoexinal strips are separated by relatively broad bands of exposed intexine (see Foster 1983), are said to be taeniate; and those in which the clefts are narrow and slitlike (e.g. *Striatoabietes*) are referred to as ribbed.

Fig. 2. A, *Striatopodocarpites* sp., specimen No. 4552/371-4-60, Aristovo, $\times 1000$. B, *Striatopodocarpites* sp., specimen No. 4388/507-39, Kotelnich, $\times 1000$. C, *Protohaploxypinus* aff. *limpidus* (Balme & Hennesly) Balme & Playford, specimen No. 4388/1-3-1-72, Mulino, $\times 1000$. D, *Lueckisporites* sp. nov. (?), specimen No. 4100/100-4-28, Vostroye, $\times 500$. E, *Piceapollenites* sp., specimen No. 3765/38-39-2, Kalinovka, $\times 1000$. F, G, pollen grains intermediate between *Lueckisporites* and *Scutasporites*: F, specimen No. 3774/5-10-92, Viled, $\times 1000$; G, specimen No. 4388/1-3-1-750, Mulino, $\times 500$.



Ribbed disaccate pollen genera

Ribbed haploxylo-noid saccate pollen of the *Protohaploxylinus*-type predominates in the assemblages and have been referred to numerous invalid genera such as *Striatolebachites*, *Striatopiceites* and *Striatopinites*. These pollen display a wide range of variability in such details as size, number of ribs and details of saccus infrastructure. Most specimens bear a general resemblance to those illustrated by Balme (1970) as *Protohaploxylinus limpidus* (Balme & Hennelly) Balme & Playford (cf. Fig. 2C) but are sufficiently different to justify regarding them as a new species. They are fairly small (50–60 µm along the longitudinal axis) with 5–8 frequently wedging ribs separated by narrow, usually branching clefts and in many specimens a short monolet tetrad scar is visible at the proximal pole. A characteristic feature of the form is that the central portion of the ribbed cappa is frequently lost in its entirety, presumably by detachment along a peripheral ring tenuitas (see Foster & Gomankov 1994). Isolated cappae, when dispersed, bear a superficial resemblance to ribbed asaccate genera such as *Vittatina*, *Fusacolpites* and *Weylandites*.

Diploxylo-noid protosaccate pollen are represented in the Tatarian by *Striatopodocarpites* (Fig. 2A), in which the sacchi are wider transversely than the corpus, and which also possess a marginal ring tenuitas on the cappa. Species of *Striatoabietites*, with longitudinally elongate corpi and relatively small, narrow sacchi are also common although they belong to a morphon that includes specimens that might reasonably be referred to *Protohaploxylinus jacobii* (Jansonius), *Protohaploxylinus samoilovichiae* (Jansonius) Hart and even, possibly, to *Lunatisporites* (= *Taeniasporites*).

Taeniate disaccate pollen

Lueckisporites, *Scutasporites* and *Lunatisporites* are the main taeniate genera, although *Lunatisporites* is not common prior to the Early Triassic Votlugian and is represented in the Tatarian only by *Lunatisporites pellucidus* (Goubin) Foster. Most

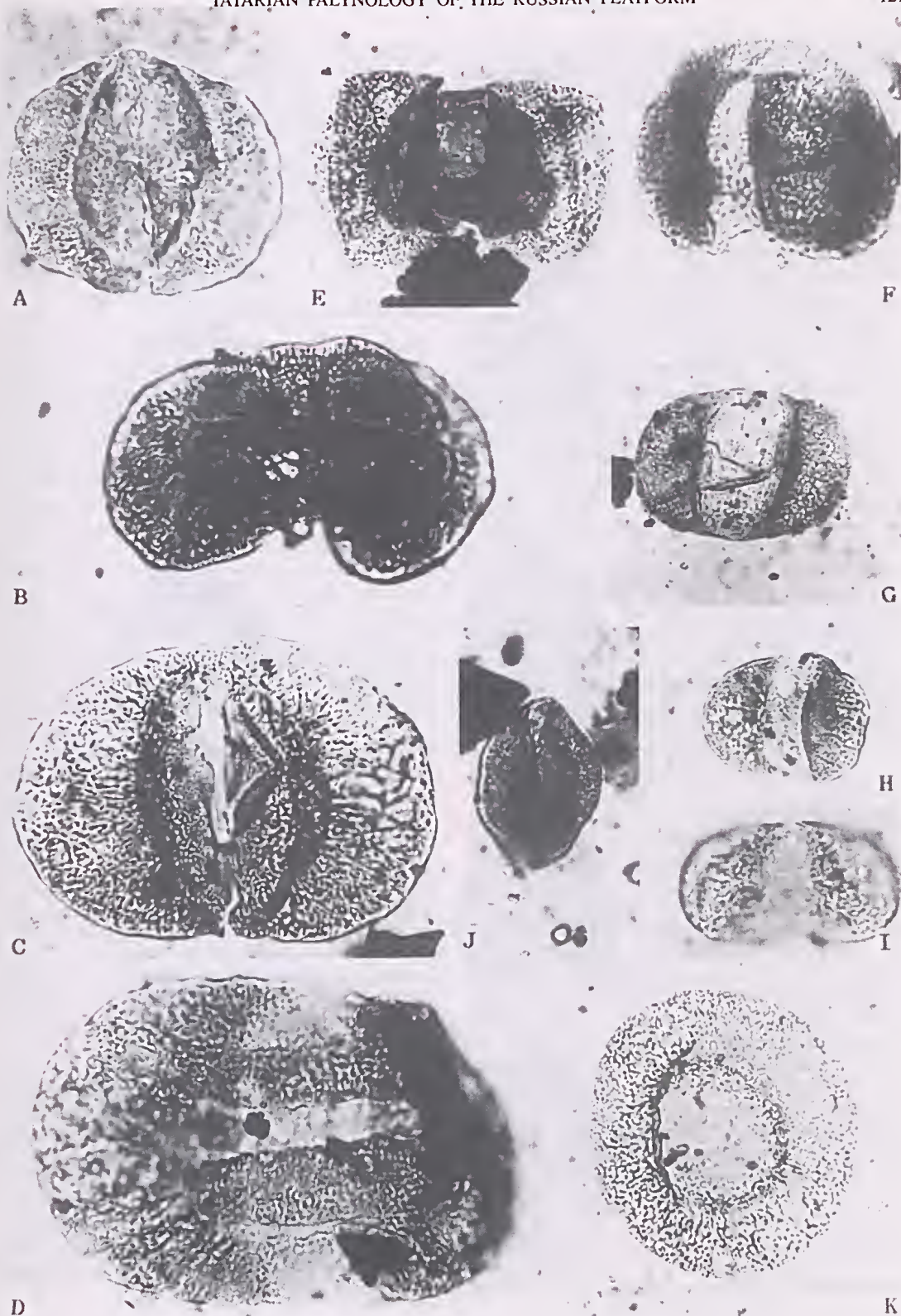
specimens of *Lueckisporites* are attributable to *Lueckisporites virkkiae* Potonié & Klaus and conform to Norm A of Visser (1971; see Fig. 3B). *Lueckisporites* Norms Bc and C, known from the middle and upper West European Zechstein (Visser 1973), are not present, which may suggest that the Tatarian is, on this evidence, older than much of the Zechstein (see further discussion below). An unusual form of *Lueckisporites* with small protosacchi (Fig. 2D) occurs in the Urzhumskian and should probably be recognised as a new species. Another Tatarian form (Figs 2F, G), that has not been recognised elsewhere, shares characters with *Scutasporites* and *Lunatisporites*. Like the former genus it is tri-taeniate but the central taenia is divided by a longitudinal cleft that reaches the margin of the cappa. It might justifiably form the basis of a new genus.

Scutasporites pollen (or more properly the plant alliance that produced it) may have evolved in the Russian Platform region during the Tatarian, from an ancestor with *Lueckisporites* pollen and subsequently colonised western Europe in Zechstein time. However, the morphographic lineage described from the European Zechstein by Visser (1971) in which he related *Lueckisporites*, *Guttulapollenites* and *Stellapollenites* cannot be traced in the Tatarian or in Angaraland. *Lueckisporites virkkiae* occurs as a stable entity throughout the Upper Permian of the Kuznetsk and Tungus Basins, where it probably ranges into the Early Triassic (Meyen 1981a; Yaroshenko 1990). This apparent stasis is another example of the phenomenon of 'extra-equatorial persistence' (see Meyen 1992).

Disaccate pollen with an entire cappa

Several form genera of disaccate pollen lacking both ribs and taeniae are prevalent in the Tatarian. Forms resembling the haploxylo-noid genus *Piceapollenites*, which could equally well be assigned to *Alisporites* (s.l.), are especially common and

Fig. 3. A, *Vesicaspora aerifera* (Andreyeva) Hart, specimen No. 3773/1458-1-3, Alexandrovka, ×1000. B, *Lueckisporites virkkiae* Potonié & Klaus, specimen No. 4100/100-4-213, Vostroye, ×1000. C, *Vesicaspora ex gr. magnalis* (Andreyeva) Hart, specimen No. 4388/1-3-1-516, Mulino, ×1000. D, *Lunatisporites pellucidus* (Goubin) Balme, specimen No. 4564/47-1-166, Luptyug, ×1000. E, *Platysaccus* sp., specimen No. 4388/1-3-1-586, Mulino, ×500. F, *Cedripites priscus* (?) Balme, specimen No. 4552/371-4-148, Aristovo, ×500. G, *Piceapollenites* sp., specimen No. 4388/1-3-1-182, Mulino, ×300. H, *Piceapollenites* sp., specimen No. 4552/371-4-108, Aristovo, ×500. I, *Vitreisporites pallidus* (Reissinger) Nilsson, specimen No. 3765/38-39-146, Kalinovka, ×1000. J, *Cladaitina*? sp., specimen No. 4388/507-80, Kotelnich, ×1000. K, *Cordaitina* sp., specimen No. 4388/1-3-1-1, Mulino, ×500.



diverse, and include several that appear to be undescribed species (Figs 2E, 3G, H). Pollen grains of the *Platysaccus*-type (Fig. 3E) are also morphologically varied.

Specimens of *Cedripites* are usually identified as *Cedripites priscus* Balme, but it would be interesting to compare them with the various species of fossil dispersed pollen grains that Zauer (1954) attributed to *Cedrus*. Two came from Kazanian sediments from the Russian Platform and one of these (*Cedrus densireticulata* Zauer) appears similar to the Tatarian form.

Specimens that are optically indistinguishable from *Vitreisporites pallidus* (Reissinger) Nilsson (Fig. 3I) are widespread and readily identifiable by their small size. Most Mesozoic specimens of *Vitreisporites* (including possibly the type species *V. signatus* Lesehik) are eaytonialean, but similar pollen has been recovered from the salpinx of the seed of a Permian peltasperm (Gomankov & Meyen 1986).

The name *Vesicaspora* has been used by workers, in Russia and elsewhere, as a broad category to include a variety of forms, many of which do not conform closely to the Carboniferous type (*Vesicaspora wilsonii* Schemel) which, although bilaterally symmetrical, is clearly monosaccate. It may also be eusaccate, as it derives, at least in part, from the Callistophytales, whose pollen are demonstrated by TEM to be eusaccate (Stidd & Hall 1970; Osborn & Taylor 1994). As far as can be judged all the Tatarian specimens referred to *Vesicaspora* are protosaccate. They fall into two groups, the first of which is provisionally designated *Vesicaspora* ex gr. *V. magnalis* (Andreyeva) Hart. It makes up a plexus of gradational forms that include specimens resembling *V. magnalis* (Andreyeva) Hart, *V. ovata* (Balme & Hennelly) Hart and *V. potonieii* (Lakhanpal, Sah & Dube) Hart, three species that need revision to determine whether they may be reliably distinguished (Gomankov & Meyen 1980). Their morphologic relationship to the Gondwanan genus *Scheuringipollenites* Tiwari also needs to be examined. Other specimens in the first group may represent undescribed species (Fig. 3C) but have not yet been studied in detail. The second group comprises the single species *Vesicaspora aerifera* (Andreyeva) Hart which is distinguished on the basis of the proportions of corpus and saecus and the characteristic structure of its exoexine.

Monosaccate pollen

Monosaccate pollen is uncommon in the Tatarian

and therefore difficult to systematise. Specimens assignable to *Cordaitina* are illustrated in Fig. 3K, and *Cladaitina*, the pollen of the rufioriaceous genus *Cladostrobus lutuginii* Zalesky, may also be present (Fig. 3J). *Cladaitina* has been previously interpreted as saecate (see Maheswari & Meyen 1975) although it does not display clear mesexinous alveolate structure and should more properly be regarded as eavate.

Ribbed asaccate pollen

Asaccate pollen grains with longitudinal proximal ribs, or modifications of ribs are for convenience almost all assigned to *Vittatina*, although a rigorous revision of their systematics is urgent. The initial problem in any reconsideration of the genus is uncertainty concerning the detailed morphology of the type species, *Vittatina subsaccata* Samoilovich ex Wilson. The holotype, which came from the Kungurian of the Cis-Urals, has been lost and is known only from a single retouched photomicrograph, taken in distal view. Koloda (1986a, 1989, and pers. comm.), who has attempted to clarify *Vittatina* systematics, believes that the leptoma in *V. subsaccata* is divided into two by a transverse exoexinal strip, as in the specimen illustrated here in Fig. 4J, or *Vittatina costabilis* Wilson (see Wilson 1962). The argument is not totally convincing however, as her SEM illustration of *V. subsaccata*, showing the subdivided distal leptoma was of a specimen from the Kazanian of the Soyana River. Further examination of topotype specimens from Samoilovich's locality is necessary to resolve these difficulties. Koloda's studies have nevertheless demonstrated that all forms of *Vittatina* have a distal leptoma which presumably functioned as an aperture, bordered by an exoexinal marginal strip. In some specimens the leptoma consists of a uniform broadly oval area, in others it is divided, as in the specimen she illustrated as *V. subsaccata* Samoilovich ex Wilson, by a transverse band of unmodified exoexine, that passes through the distal pole.

Diversity within the *Vittatina*-complex is mainly manifested by variations in the patterns developed in the distal marginal exoexine and its distribution in relation to the leptomate areas. They fall into the following categories:

(a) Specimens with an unpatterned leptoma and exoexine (Figs 4a, b, i) and in which the marginal exoexinal strip either maintains a constant width (Figs 4a, i) or is expanded at the longitudinal extremities of the grain (Fig. 4b).

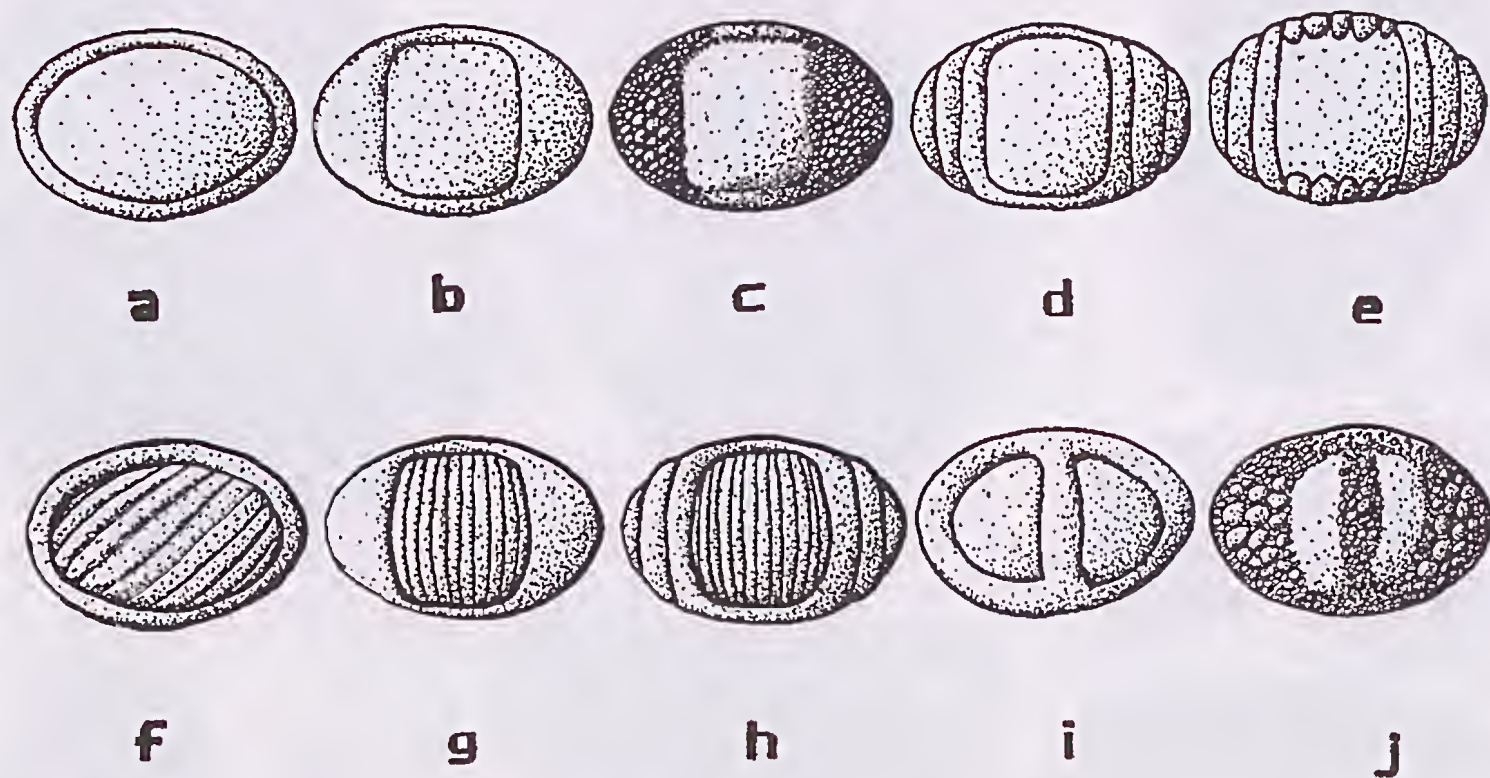


Fig. 4. Diversity of the distal surface of *Vittatina*-like pollen grains (see text for details).

(b) Grains in which the leptoma is unpatterned but the exoexine is subdivided by narrow sub-parallel or anastomosing clefts which create patterns of transverse ribs (Figs 4d, e) or pseudoverrucate (Figs 4c, j). The pattern may be present on the entire distal exoexine (Fig. 4e), or confined to expansions in the longitudinal area (Fig. 4d). In their broad morphography the grains illustrated by Fig. 4d resemble the genus *Weylandites* Bharadwaj & Srivastava, but Foster et al. (1994) compared examples of the Gondwanan genus with similarly structured Angaran specimens of *Vittatina* and demonstrated that they differ in details of exoexinal structure. In the Gondwanan species the ribs appear smooth and structureless, whereas those in the Angaran show a faint scabrate pattern reflecting the fine perforation of the exoexine observed by Koloda (1986a).

(c) Specimens with patterns of faint transverse (Figs 4g, h) or oblique ribs (Fig. 4f) within the leptoma. Koloda (1986a) proposed the generic name *Duplivittatina* to accommodate such forms but it has not yet been validly published. The grains illustrated in Figs 4a–c conform to the genus *Ventralvittatina* Koloda, although, as implied earlier, the distinction between this taxon and *Vittatina* (s.s.) needs elucidation.

(d) In several forms, subprotosacci are present at the lateral extremities of the exoexine (Figs 4b, e, g, j), apparently as a result of differential thickening, following the development of mesexinous alveolate tissue. The same feature was discussed by Abramova & Marchenko (1964) who suggested that there was a continuous transition from *Vittatina* to protodisaccate genera such as *Striatoabieites*.

Ribbed asaccate pollen grains are almost as common in the Tatarian as *Protohaploxypius*, but less obviously varied. Specimens referable to *Ventralvittatina vittifera* (Luber) Koloda (Fig. 5F) and *Vittatina elegans* Zauer ex Varjuchina (Figs 5I, J) are characteristic of the Urzhumskian. In the

Severodvinskian and Vyatskian the most abundant variants of *Vittatina* have pseudoverrucate ribs and a transverse band of exoexine dividing the leptoma (Fig. 6D) and have usually been assigned to *Vittatina subsaccata* f. *connectivalis* Zauer. However, if Koloda is correct in her interpretation of the structure of Samoilovich's holotype, the name *V. subsaccata* f. *connectivalis* is superfluous and they should be simply designated *V. subsaccata*. The Severodvinskian and Vyatskian also yield rare specimens which are recognised as new species of *Weylandites*: *W. tataricus* Gomankov (Figs 5A, B; see Gomankov 1996) and *Weylandites* sp. (Fig. 5C).

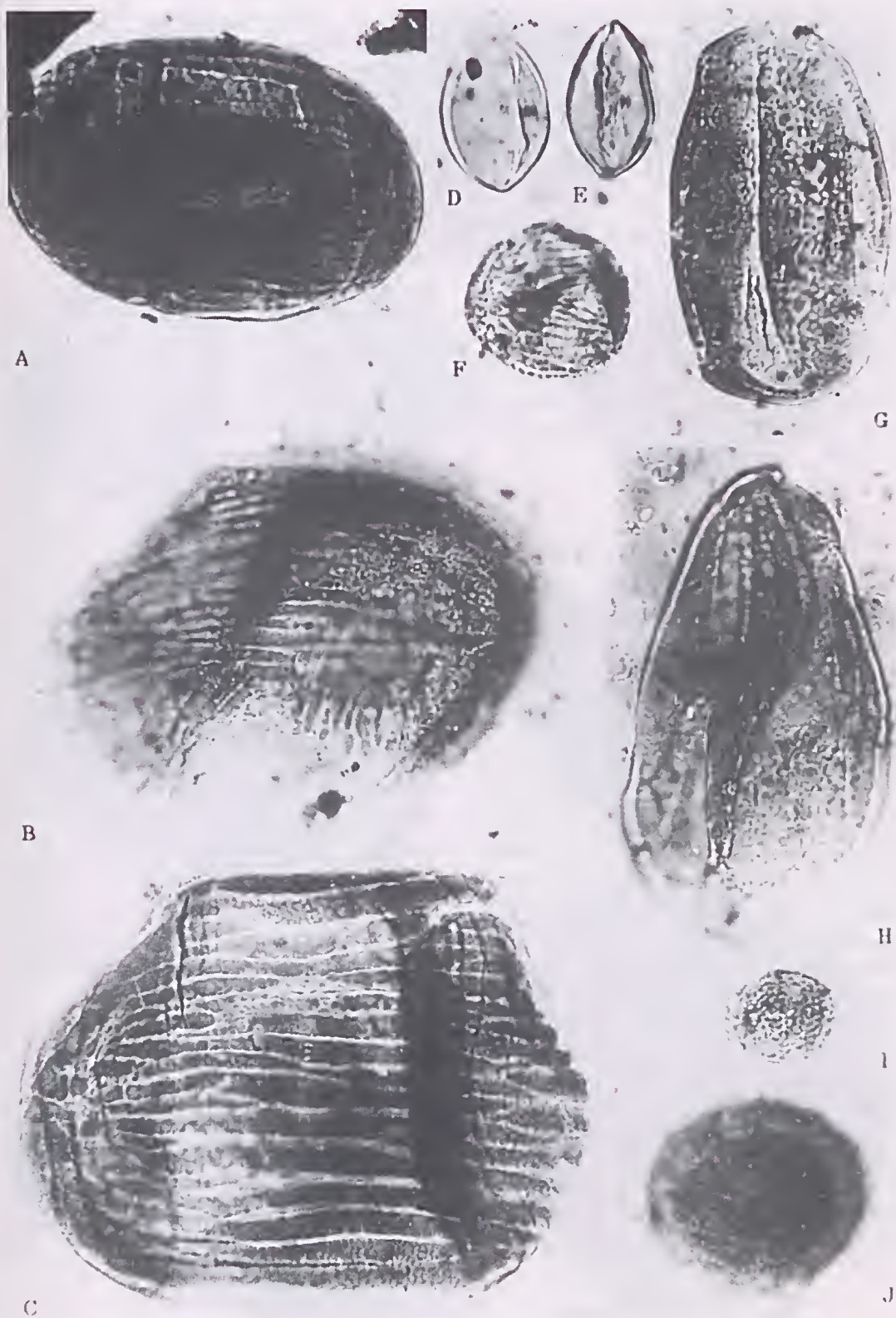
Sulcate pollen

Two types of sulcate pollen occur sporadically in the Tatarian. One is a form of *Cycadopites* with a scabrate margo (Figs 5D, E) that appears to differentiate it from any existing species. The other (Figs 5G, H) is a radiosymmetrical, quadrisulcate, grain broadly similar to *Praecolpatites* Bharadwaj & Srivastava but sufficiently distinct in geometric form to justify its recognition as a new genus, *Mulinopollenites* (for details see Gomankov 1996).

Cryptogam spores

Relative to ribbed and taeniate pollen, spores are minor and poorly diversified components of Tatarian assemblages. Simple radiosymmetrical trilete forms are the most common. Some with a circular amb are smooth and similar to, but smaller and with shorter laesura than, *Calamospora landiana* Balme (Fig. 6C), others bear small, closely packed coni and conform to *Osmundacidites* (Fig. 6J). Unstructured specimens with a triangular amb belong predominantly to *Neoraistrickia* and bear a sculpture of heavy bacula (Fig. 6A), but an unusual form, *Brevitriletes subangaricus* Gomankov (1996; Figs 6G, H) with a distal sculpture of large contiguous coni and a smooth proximal face, is present in small numbers.

Fig. 5. A, B, *Weylandites tataricus* Gomankov (cf. Fig. 4e), $\times 1000$: A, specimen No. 4388/507-154 in polar view, Kotelnich; B, specimen No. 4364/47-1-24 in equatorial view, Luptyug. C, *Weylandites* sp. nov. 2 (cf. Fig. 4d), specimen No. 3774/5-10-183, Vilcd, $\times 1000$. D, E, *Cycadopites* sp. nov. (?), specimens Nos. 3765/38-39-74 and 3765/38-39-51, Kalinovka; $\times 1000$. F, *Ventralvittatina vittifera* (Luber) Koloda, specimen No. 4100/100-4-145, Vostroye, $\times 1000$. G, H, *Mulinopollenites bonus* Gomankov, Mulino, $\times 1000$: G, specimen No. 4388/1-3-1-183; H, specimen No. 4388/1-3-1-67. I, J, *Ventralvittatina elegans* (Zauer ex Varjuchina), specimen No. 4100/100-4-226, Vostroye: I, $\times 500$; J, $\times 1000$.



Structured trilete spores include cingulate forms resembling *Limnolasporites fossulatus* (Balme) Foster & Helby (Fig. 6F) and zonate specimens that may represent an undescribed species of *Kraeuselisporites* (Fig. 6I). The simple monolete genus *Punctatosporites* is represented by a small, finely scabrate species (Fig. 6B).

Palynomorphs of uncertain origin

Alete, subcircular or distorted bodies (Fig. 6E) of uncertain origin occur fairly commonly and persistently. They are variable in size, and in the thickness and pattern of folding of the wall. They have usually been considered to be pollen grains and recorded as *Azonaletes* or *Laricoidites*, but an algal origin is equally likely and it would be more appropriate to treat them as leiosphaerid acritarchs.

AFFINITIES OF DISPERSED PALYNOMORPHS

General

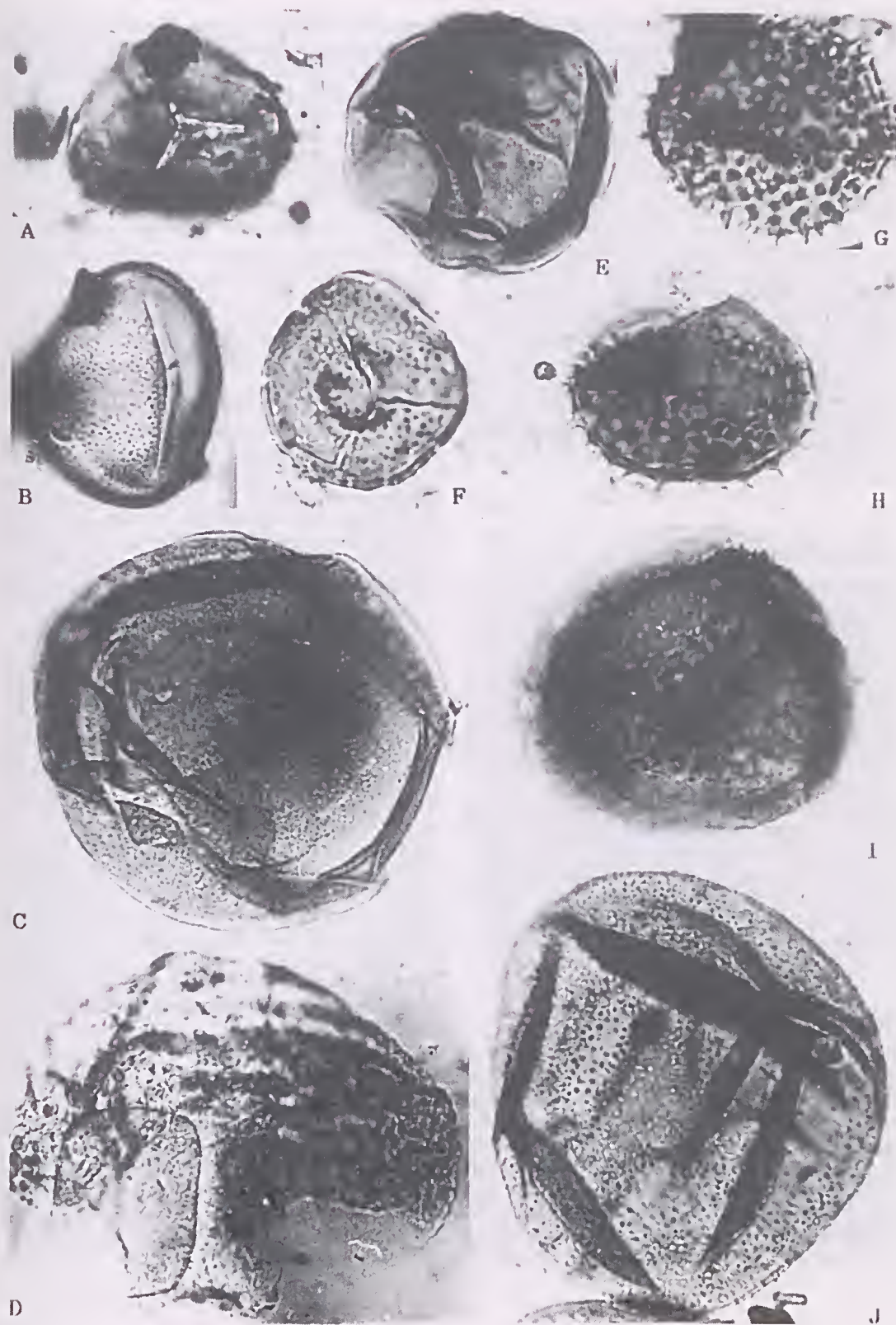
Few fossil plant localities are known from the Urzhumskian but several comprehensive accounts (Gomankov & Meyen 1986; Gomankov 1986; Gomankov et al. 1986) deal with macrofossil floras of the Severodvinskian and Vyatskian Horizons, the so-called Tatarina-Flora. In these studies special emphasis was paid to *in situ* (or *juxta in situ*) occurrences of spores and pollen grains. These were extracted from sporangia and seed micropyles and some coprolites were also processed. Data obtained have enabled some generalisations concerning the composition of late Tatarian floras (Gomankov 1992a) as at each collecting locality the order of abundance of the various macrofossil groups matches that of their related dispersed microfossil taxa. This suggests that in the absence of macro-

fossils it may be possible, at least in some situations, to use palynomorphs to assess the broad composition of their parent plant communities. Such extrapolation obviously has limitations, however, as it requires detailed knowledge of the affinities of the dispersed palynomorphs and clear understanding of the sedimentary mechanisms by which they were deposited.

Ribbed pollen

Peltasperms from which the leaf genus *Tatarina* and the female structure *Peltaspermopsis* derived are thought to have produced pollen of both the *Protophloxypinus*- and *Vittatina*-type. The evidence is convincing although still indirect. The synangium *Permothea striatifer* Gomankov & Meyen occurs in constant association with *Tatarina* although it is not known in direct attachment. It has yielded pollen resembling *Protophloxypinus limpidus*, as well as occasional specimens of the *Striatopodocarpites*-type. Such variability is unsurprising but serves as a reminder that minor differences in the morphography of fossil dispersed (particularly saecate) pollen may have no significant biological implications. Pollen referable to *P. limpidus* (s.l.) has also been recovered from the micropyle of *Salpingocarpus bicornutus* Meyen and *Salpingocarpus variabilis* Meyen. *S. variabilis* ovules are known from specimens in organic connection with *Peltaspermopsis* fructifications, which are inferred to belong to the same plant as *Tatarina* leaves, because of their closely similar epidermal structures and constant stratigraphic association. Another interesting occurrence of abundant *P. limpidus* (s.l.; see Fig. 2C) in association with *Tatarina*-type cuticles, was in a small coprolite described by Gomankov et al. (1986). Although not impossible, it seems unlikely that the browsing herbivore was selectively eating leaves from one plant and sporangia from another, and so it is a reasonable inference that the pollen and cuticles came from the same plant.

Fig. 6. A, *Neoraistrickia*? sp., specimen No. 4388/507-83, Kotelnich, $\times 1000$. B, *Punctatosporites*? sp., specimen No. 3782/252a-177, Titovo, $\times 1000$. C, *Calamospora* aff. *landiana* Balme, specimen No. 4552/371-4-70, Aristovo, $\times 1000$. D, *Vittatina subsaccata* Samoilovich, pollen grain in equatorial view (cf. Fig. 4j), the rectangular contour at the lower left is an imprint of pyrite crystal, specimen No. 4388/1-3-1-17, Mulino, $\times 1000$. E, *Laricoidites* sp., specimen No. 4564/47-1-54, Lutyug, $\times 1000$. F, ?*Limnolasporites fossulatus* (Balme) Helby & Foster, specimen No. 3774/3-a-49-22, Viled, $\times 1000$. G, H, *Brevitriletes subangaricus* Gomankov, Mulino, $\times 1000$: G, spore in polar view, specimen No. 4388/1-3-1-328; H, spore in equatorial view, specimen No. 4388/1-3-1-473. I, *Kraeuselisporites* sp. nov. (?), specimen No. 4552/371-4-184, Aristovo, $\times 1000$. J, *Osmundacidites*? sp. nov., specimen No. 4388/1-3-1-412, Mulino, $\times 1000$.



Peltasperms also produced *Vittatina*-type pollen. It has been found in masses beneath the cupulate heads of two specimens of *Peltaspermopsis buevichiae* (Meyen & Gomankov) Gomankov (cf. Fig. 6D) and, at the same locality, in the sporangium *Permothea ?vittatinifera* Meyen & Gomankov and in ovules of *Salpingocarpus variabilis* in association with *Protohaploxylinus*. The fact that at least some specimens of *Vittatina* and *Protohaploxylinus* were probably produced by the same plants might be expected, in view of the many examples of dispersed pollen showing characters transitional between the two genera. It must of course be emphasised that *Vittatina* and *Protohaploxylinus* first appear in the Carboniferous (Dyupina 1975) and that the latter genus has also been recorded *in situ* from Gondwanan glossopterid sporangia (Pant & Nautiyal 1960). Their occurrence as dispersed specimens cannot therefore be regarded as specific evidence for the undoubted presence of peltasperms.

Taeniate disaccate pollen

Lueckisporites has been recorded *in situ* from Permian and Triassic conifers and putative conifers in Western Europe (Clement-Westerhof 1987; Klaus 1966). Meyen (1981a) suggested that some species of the lebachiacean *Quadrocladus* also produced this pollen-type, based on the intimate association between both remains, including pollen adhering to cuticle, from some Siberian localities. Later work on Tatarian assemblages from the Russian Platform discovered many grains transitional between *Lueckisporites* and *Scutasporites*, confirming the initially suggested association. *Scutasporites unicus* Klaus is present in sporangia of the lebachiacean microstrobilate structure *Dvinostrobilus sagittalis* Gomankov & Meyen, which is in turn related through comparison of cuticular characters, to *Quadrocladus* foliage and *Sasthinia* polysperms.

Disaccate pollen with an entire cappa

Pollen from the cardiolepidaceous sporangium *Permothea vesicasporoides* Meyen, Esaulova & Gomankov is protodisaccate, haploxylonoid, with a distal sulcus (Meyen, Esaulova & Gomankov, in Gomankov & Meyen 1986) and strictly conforms to the genus *Falcisporites*, but it also falls within the concept of *Vesicaspora* ex gr. *magnalis* used earlier in this account (cf. Fig. 3C). Esaulova's specimens were from the Kazanian of the Kama region, and occurred in association with macrofossil

plant remains consisting entirely of *Phylladoderma* leaves. Similar sporangia containing the same pollen are present in the Tatarian, where they are also associated with *Phylladoderma* leaves, which are recognised as the separate subgenus *Aequistonia*. The peltate capsule *Cardiolepis* and the seed *Nucicarpus* are also thought to belong to the same plant.

There is some indirect evidence, from their constant association, that *Vesicaspora aerifera* and the small-leaved (Meyen's sulcial) cordaitanthalean foliage *Cordaites clericii* Zalesky, derived from the same plant. On the Russian Platform the leaves are known from only one Tatarian locality, where *V. aerifera* is also abundant, although elsewhere in the Russian Permian sulcial cordaitanthalean leaves usually occur together with monosaccate pollen of the *Cordaitina*-type. The fact that *Potonieisporites* and *Cordaitina*, the two monosaccate genera known to have been produced by cordaitanthaleans, are entirely absent from the locality of *C. clericii* also provides some negative support for its relationship with *V. aerifera*. It is perhaps significant too that the type locality of *V. aerifera*, in the lower part of the Upper Permian Leninskaya Suite in the Kuznetsk Basin (Andreyeva et al. 1956), yielded a variety of sulcial cordaitanthalean foliage.

Monosulcate pollen

Little can be confidently inferred concerning the biological affinities of the dispersed monocolpate genus *Cycadopites* (Figs 5D, E), at least in the absence of TEM data. It is especially abundant at one Tatarian locality where the remains of the presumed leptostrobalean leaves *Sphenarion* are common and it is also possibly the pollen of peltasperms with *Glossophyllum* foliage and *Stiphorus* polysperms. *Cycadopites* has been recorded *in situ* from the peltaspermaceous microstrobilis *Antevsia* (Townrow 1960; see Balme 1995 for summary), but similar pollen is known to have been produced by extinct members of the Ginkgoales, Bennettitales, Cycadales, Gnetales, Pentoxylales and magnoliopsids.

Cryptogam spores

By inference, the dispersed specimens of *Calamospora* are degraded spores of equisetopsids, stems of which are represented in the Tatarian by *Neocalamites*. The *Kraeuselisporites*-type zonate spores (Fig. 6I) are characteristically lycopsid and may have originated from the plants that possessed *Fasciostomia* leaves.

All known fossil *in situ* occurrences of the genus *Punctatosporites* are from marattiaceous synangiate structures, so there is little doubt that the small forms present here were the spores of a member of the Marattiaceae, which probably produced the foliage from the upper Vyatskian described as *Pecopteris* sp. by Gomankov & Meyen (1986). *Osmundacidites* and *Neoraistrickia* are almost certainly filicopsid but their closer affinities cannot be judged.

TATARIAN PALYNOSTRATIGRAPHIC SEQUENCE

Tatarian playnomorph assemblages do not differ in any obviously essential way from those of the Kazanian, and no apparent aspects of Tatarian palynology enable plant microfossils to provide a reliable zonal scheme for any precise biostratigraphic subdivision of the Stage. The assemblages certainly vary widely in both their quantitative and qualitative compositions, but these variations cannot be securely interpreted at the level of current understanding of the factors that influence them. Throughout the succession it is possible to identify, with a degree of subjectivity, a few broad trends in the relative abundances of certain forms and on this basis the following sequence of four palynological assemblages—zones has been tentatively recognised, although they have not been formally named.

Zone I

This occurs in strata corresponding roughly to the Urzhumskian. Its lower boundary marks the disappearance of *Haniapollenites* and *Limitisporites* and the appearance of pollen of the *Weylandites*-type with a wide distal leptoma, species of *Lueckisporites* (including *L. virkkiae* and a distinctive undescribed form with greatly reduced sacci) and the large ribbed disaccate species *Protohaploxypinus samoilovichiae* and *Lunatisporites pellucidus*. Variants of *Vittatina*, including *V. elegans* and those that Koloda described as *Ventralvittatina* (*V. vittifer*) and *Duplivittatina* spp. are characteristic elements of this zone.

Zone II

The second zone is found in the lower part of

the Severodvinskian Horizon. *Ventralvittatina* and *Duplivittatina* are no longer present, nor is the heteromorph of *Lueckisporites* with small sacci. The earliest occurrence of *Vesicaspora aerifera* and spores resembling *Limatulasporites fossulatus* are in this assemblage where they are associated with the presumed cordaitalean pollen genera *Cladaitina*, *Cordaitina* and 'Florinites'.

Zone III

This spans the upper Severodvinskian and lower Vyatskian. Its assemblages are similar to those of Zone II except that they contain very few examples of *Cladaitina*, *Cordaitina* and 'Florinites' and *Neoraistrickia* sp. is also very rare. A few specimens of *Scutasporites unicus* Klaus have also been recorded from this Zone.

Zone IV

Cedripites priscus, *Mulinopollenites bonus*, *Kraeuselisporites* sp. and *Punctatosporites* sp. appear for the first time in the upper Vyatskian Horizon. These species are all fairly distinctive and provide a firmer basis for a provisional definition of the Zone than do the criteria that characterise Zones I–III.

The magnitude of the stratigraphic hiatus between the Tatarian and overlying Vettugian on the Russian Platform has been the subject of some controversy. Gomankov (1992a) suggested that the break represented almost all of the Upper Permian Dzulfian and Dorashamian Stages as well as the basal Griesbachian, a time span of about 5 million years. Others believe the interval to be considerably shorter. Lozovskiy (1992) correlated the Tatarian with the Dzulfian, and Foster & Jones (1994) used evidence from conchostracans and palynology to argue that it also encompassed much of the Dorashamian.

Whatever the resolution of this debate there is no question that a strong palynological break occurs between the Vyatskian and Vettugian. It is marked by the virtual disappearance of *Vittatina* and a sharp decline in *Protohaploxypinus*. Species of *Lunatisporites* are abundant in the Vettugian, *Ephedripites*, *Cycadopites* and *Strotersporites* are common and *Klausipollenites schaubergeri* occurs for the first time. The lycopsid spore genera *Densoisporites* and *Lundbladisporea* are also significant, as they are in Early Triassic assemblages throughout the World.

RELATIONS BETWEEN PLANT MICROFOSSIL AND MACROFOSSIL REMAINS

Data on plant macrofossils and their distribution in the Tatarian of the Russian Platform are uneven. Disparate and well-preserved associations of fronds, axes, reproductive structures and other plant entities are known from the many localities in the Severodvinskian and Vyatskian (Gomankov & Meyen 1986). Bryophytes, lycopsids, equisetopsids and filicopsids are well represented but the floras are particularly characterised by an abundance and diversity of peltasperms and conifers. By contrast few plant fossil localities have been found in the Urzhumskian and the floras, although less well documented, appear impoverished relative to those of the upper Tatarian. They are dominated by odontopteroid and dicranophylloid foliage and shoots referred tentatively to *Geinitzia*.

The pronounced differences between macrofossil floras from the lower and upper Tatarian are not, as was noted earlier, matched in the palynofloras, which are essentially similar throughout the succession. This could simply reflect taphonomic factors, in that the dispersed plant microfossils were principally produced by plants which otherwise left no fossil record and that the macrofossils belonged to specialised plant communities, growing in circumstances that favoured their selective preservation. However, at least in the upper Tatarian, there appears to be a significant correspondence between the abundance of particular pollen taxa and macroscopic fragments of the plants that were believed to have produced them (e.g. *Tatarina* and the *Protohaploxypinus-Vittatina* complex). This suggests that, to some degree, the palynomorphs and plant megafossils that occur together represent remains of the same plants. If this is also true of the early Tatarian associations, it must be assumed that the parent plants of the older specimens of *Protohaploxypinus* and *Vittatina* were peltasperms that bore odontopteroid foliage. If so, the implications are that evolution within this lineage of the Peltaspermales was manifested by rapid phenotypic response in foliar organs, while the pollen morphology remained conservative.

COMPARISON WITH LATE PERMIAN ASSEMBLAGES FROM ELSEWHERE

Utting & Piasecki (1995) provide a comprehensive account of Permian palynofloras of the Northern Hemisphere, and as a consequence our review here

is limited. The Late Permian was a time maximum global palaeofloristic differentiation (Meyen 1987), and therefore few close correspondences between plant microfossil assemblages from widely separated geographical regions might be predicted. But we also note that global palynological data have not yet been fully and critically assessed. Moreover, the quantitative composition of recovered spore-pollen floras, even within a single plant province, can fluctuate markedly, reflecting effects of environmental, preservational or evolutionary pressures on the parent flora: the difficulty is in distinguishing, time significant events.

Primacy for correlation may be given to first appearance datums (FAD), although use of FADs can be selective. In this study for example the FAD of *Scutasporites* is in Zone III, but in East Greenland *Scutasporites* first appears in the *Vittatina*-Assemblage (Balme 1979), which, compositionally, is most like older Zone I palynofloras from the Urzhumskian Horizon.

In the Late Palaeozoic the Russian Platform formed part of the transitional Sub-Angaran palaeofloristic province, which extended around the margins of Angaraland (Meyen 1987; Gomankov & Meyen 1986). Palynological assemblages generally sharing common features with those of the Upper Permian of the Russian Platform and Urals Foredeep have been described from East Greenland (Balme 1979; Piasecki 1984), Svalbard (Mangerud & Konieczny 1993), the Finnmark Platform, Barents Sea (Mangerud 1994), and the Canadian Arctic Archipelago (Utting 1989, 1994). Because of uncertainties concerning the chronostratigraphic relationships of the Tatarian with these Arctic sequences, it is difficult to interpret the palynological data in palaeofloristic terms.

The *Vittatina*-Assemblage of East Greenland (Balme 1979), is characterised by the high content (7–37%) of various species of *Vittatina*, by the taeniate disaccate pollen of *Protohaploxypinus*, *Striatoabieites* and *Lunatisporites* (al. *Taeniaesporites*), and the virtual absence of trilete spores. Quantitatively it is undoubtedly similar to the associations found in Zone I, described from the Urzhumskian. But as noted above, members of the genus *Scutasporites* (the key to younger Zone III) also occurs in the *Vittatina*-Assemblage, in association with the ammonoid *Cyclolobus* which indicates a Dzulfian age (see Utting & Piasecki 1995; Nassichuk 1995). We are left with the dilemma: are the correlative Russian Zone I palynofloras of Dzulfian age, or using the current FAD of *Scutasporites*, is the base of Zone III (from the upper Severodvinskian and lower Vyatskian) of Dzulfian age. Alternatively, the true FAD for

Scutasporites on the Russian Platform may not yet be established. At present correlation with Zone I/1 is favoured.

Studies from the Permian of Arctic Canada (Utting 1989, 1994; Utting et al. 1997) show that the FAD of *Scutasporites* occurs in older rocks of Wordian age (Kazanian correlatives based on faunal evidence—see Utting 1994). Utting et al. (1997) compared palynofloras from older (pre-Tatarian) Ufimian–Kazanian type sequences of the Russian Platform with those from the Canadian Arctic and other circumpolar areas such as the Barents Sea and Greenland. They concluded that significant palaeoclimatic differences affected the respective parent floras, such that ‘there is little basis for correlation’ ... based on palynofloras.

Mangerud (1994) has provided comprehensive and excellently illustrated documentation of the palynology of Permian and Lower Triassic strata encountered in offshore drillholes on the Finnmark Platform, Barents Sea. The youngest Permian strata are equivalent to the upper part of the Tempelfjorden Group and encompass Biozone XV (Bugge et al. 1995), which was correlated by Mangerud (1994) with the Kazanian(?)–Tatarian of the Russian Platform. The upper age range (?Tatarian) for the *Scutasporites* sp. cf. *S. uticus*–*Lunatisporites* sp. Concurrent Range Zone, is based on the Russian (Tatarian) records of *Scutasporites*, *Lunatisporites* and *Lueckisporites virkkiae* (Mangerud 1994). But precise correlation with Zones I–IV is not yet possible. Correlation with other European Permian palynofloras, including those from the Zechstein, is discussed by Utting & Piasecki (1995).

From the spore-pollen assemblages of the Chhidru Formation, Salt Range, Balme (1970) suggested that the parent flora ‘appears to have transitional characters and includes Gondwanid, European, Russian and Madagascan elements’. This was a pivotal study allowing correlation between the different phytogeographic provinces. Taxa in common with the Tatarian include gymnosperm pollen (*Lueckisporites virkkiae*, *Lunatisporites noviaulensis*, *Vitreisporites pallidus*), and amongst the trilete spores, particularly from Zone IV, *Limatulasporites* (al. *Nevesisporites*) *fossulatus*, *Kraeuselisporites* spp., *Osmundacidites senectus* and *Calamospora landiana*. There are however significant differences in some miospore age-ranges: taxa from the Upper Chhidru (*Klausipollenites schaubergeri*, *Densoisporites*, *Lundbladispora*) appear on the Russian Platform only in the Early Triassic. Again no precise correlation is possible, and further study is needed urgently.

Tatarian spore-pollen taxa have been recognised

in more remote phytogeographic provinces, namely Cathaysia and Gondwana (e.g. Ouyang 1982; Foster 1979; Foster et al. 1994). However, because known plant macrofossils from these respective phytogeographic provinces (Sub-Angara, Cathaysian, Gondwanan) are morphologically different, and it has been shown that different plant groups may produce apparently identical pollen, the occurrence of shared taxa has been attributed to convergence (or parallelism; see Meyen 1981b, 1982). Remark- ing on this phenomenon, Utting & Piasecki (1995) concluded ‘Although such convergence may have occurred, it seems unlikely that it would have been widespread. An alternative explanation may be that unrecognised affinities exist between plant groups from Gondwana and Sub-Angara.’

Whatever the answer, these views emphasise the need for continuing, active, and international studies of the both palynofloras and associated macroflora.

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REFERENCES

- ABRAMOVA, S. A. & MARCHENKO, O. F., 1964. On the question of the classification of forms of *Vuutina* Lub. and forms with striate body and sacci. In *Systematics and methods of studying of fossil pollen and spores*, Nauka Press, Moscow, 49–52. (In Russian.)

- ANDREYEVA, E. M., MANDELSTAM, M. O., RADZENKO, G. P., ROTAI, A. P., KHALFIN, L. L. & YAVORSKY, V. I., 1956. *Atlas of leading forms of fossil flora and fauna of the Permian System of the Kuznetsk Basin*, Gosgeoltekhizdat Press, Moscow, 411 pp. (In Russian.)
- BALME, B. E., 1970. Palynology of Permian and Triassic Strata in the Salt Range and Surghar Range, West Pakistan. In *Stratigraphic boundary problems: Permian and Triassic of West Pakistan*, University of Kansas, Department of Geology Special Publication 4, The University Press of Kansas, 304-453.
- BALME, B. E., 1979. Palynology of Permian-Triassic boundary beds at Kap Stosch, East Greenland. *Meddelelser om Grønland* 200: 1-37, pls 1-3.
- BALME, B. E., 1995. Fossil and in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology* 87: 81-323.
- BUGGE, T., MANGERUD, G., ELVEBAKK, G., MORK, A., NILSSON, I., FANAVOLL, S. & VIGRAN, J. O., 1995. The upper Palaeozoic succession on the Finnmark Platform, Barents Sea. *Norsk Geologisk Tidsskrift* 75: 3-30.
- CLEMENT-WESTERHOF, J. A., 1987. Aspects of Permian palaeobotany and palynology, VII. The Majonicaceae, a new family of Late Permian conifers. *Review of Palaeobotany and Palynology* 52: 375-402.
- DYUPINA, G. V., 1975. The morphology and stratigraphic distribution of striated pollen in Permian deposits of the central Urals. In *New miospores, foraminifers, ostracods and conodonts of the Palaeozoic and Mesozoic of the Urals. Collection on the problems of stratigraphy* No. 24. (Trudy Instituta geologii i geokhimi, Ural'skii nauchn'i tsentr, Akademiya Nauk SSR.) *Transactions of the Institute of Geology and Geochemistry of the Uralian Scientific Centre of the Academy of Sciences of the USSR* 119: 28-55. (In Russian.)
- EFREMOVA, G. D., 1966. On the classification of the dispersed pollen of Striatiti Pant, 1954. In *On the methods of the palaeopalynological studies. Materials for the 2nd International Palynological Conference*, Leningrad, 42-57. (In Russian.)
- FOSTER, C. B., 1979. Permian plant microfossils of the Blair Athol Coal Measures, Baralaba Coal Measures, and basal Rewan Formation of Queensland. *Geological Survey of Queensland, Publication 372, Palaeontological paper* 45, Brisbane, 1-244.
- FOSTER, C. B., 1983. *Jugasporites* Leschik 1956, a Late Palaeozoic operculate pollen genus. *Memoir of the Association of Australasian Palaeontologists* 1: 327-338.
- FOSTER, C. B. & GOMANKOV, A. V., 1994. A new structure in pollen assigned to *Striatopodocarpites* Sedova 1956 and *Protolaploxyrinus* Samoilovich emend. Morbey, 1975, from the Late Permian (Tatarian) of the Russian Platform. *AGSO Journal of Australian Geology & Geophysics* 15: 235-238.
- FOSTER, C. B. & JONES, P. J., 1994. Correlation between Australia and the type Tatarian, Russian Platform, evidence from Palynology and Conchostraca: a discussion. *Permian* 24: 36-43.
- FOSTER, C. B., GOMANKOV, A. V., YAROSHENKO, O. P., DYUPINA, G. V. & FADDEEVA, I. Z., 1994. Analysis of selected 'shared' miospores from the Permian and Early Triassic of Russia and Australia: preliminary report. *Geological Society of Australia, Abstracts* 37: 113-114.
- GOMANKOV, A. V., 1986. The affinity of Permian miospores. In *The theory and practice of the palynological studies of Permian and Triassic of the USSR*. Manuscript deposited at the All-Union Institute for Scientific and Technical Information (VINITI, Vsesoyuznyi Institut Nauchnoi i Tekhnicheskoi Informatsii), No. 4839-B86, Syktyvkar, 4-9. (In Russian.)
- GOMANKOV, A. V., 1992a. The interregional correlation of the Tatarian and the problem of the Permian upper boundary. *International Geology Review* 34: 1015-1020.
- GOMANKOV, A. V., 1992b. The relationship between plant micro- and megafossil assemblages: an environmental signal in the uppermost Permian of the Russian Platform. In *Organisation Internationale de Paleobotanique, IVeme Conference*, Paris, 1992. Resumes des communications. *O.F.P. Informations*, N special 16-B. Paris, p. 68.
- GOMANKOV, A. V., 1996. Palynological and floristic characteristics of the Tatarian Stage. In *Stratotypes and reference sections of the Upper Permian of regions of the Volga and Kama Rivers*, N. K. Esaulova & V. R. Lozovsky, eds, Kazan State University, Kazan, 365-380. (In Russian.)
- GOMANKOV, A. V., KYUNTZEL, M. K. & MEYEN, S. V., 1986. *New data on the plant remains from the Upper Permian and Lower Triassic of the Russian Platform*. Manuscript deposited at the All-Union Institute for Scientific and Technical Information as an appendix to Transactions of the Geological Institute of the Academy of Sciences of the USSR, 401 (VINITI, Vsesoyuznyi Institut Nauchnoi i Tekhnicheskoi Informatsii) No. 7994-B86, Moscow, 86 pp. (In Russian.)
- GOMANKOV, A. V. & MEYEN, S. V., 1980. On the relationships between assemblages of plant mega- and microfossils in the Permian of Angaraland. *Palaeontological Journal* 4: 114-122. (In Russian.)
- GOMANKOV, A. V. & MEYEN, S. V., 1986. Tatarina-flora (composition and distribution in the Late Permian of Eurasia). *Transactions of the Geological Institute of the Academy of Sciences of the USSR* 401: 174 pp. (In Russian.)
- GORBATKINA, T. E. & STOK, N. I., 1984. The geological structure of the Tatarian. In *The Upper Permian and Lower Triassic deposits of the Moscow Syncline*, Nedra Press, Moscow, 4-55. (In Russian.)
- IGNATIEV, V. I., 1962. *Tatarian stage of the central and eastern regions of the Russian Platform. Part I. Stratigraphy*. Kazan University, Kazan, 334 pp. (In Russian.)

- IGNATIEV, V. I., 1963. *Tatarian stage of the central and eastern regions of the Russian Platform. Part II. Facies, palaeogeography*. Kazan University, Kazan, 338 pp. (In Russian.)
- IGNATIEV, V. I., 1987. Late-Permian lakes of Volga-Ural anticline. In *The history of lakes of the Upper Palaeozoic and Lower Mesozoic*, G. G. Martinson & I. J. Neustrueva, eds, Nauka Press, Leningrad, 140-148. (In Russian.)
- JIZBA, K. M. M., 1962. Late Paleozoic bisaccate pollen from the United States midcontinent area. *Journal of Paleontology* 36: 871-887.
- KLAUS, W., 1966. Zwei Pflanzenreste der alpinen Trias mit ihren Sporen (*Lueckisporites* und *Decussatisporites*). *Geologische Bundesanstalt (Austria)* 1-2: 172-177.
- KOLODA, N. A., 1986a. On the problem of the classification of vittatins. In *The theory and practice of the palynological studies of Permian and Triassic of the USSR*. Manuscript deposited at the All-Union Institute for Scientific and Technical Information (VINITI, Vsesoyuznyi Institut Nauchnoi i Tekhnicheskoi Informatsii) No. 4839-B86, Syktyvkar, 9-12. (In Russian.)
- KOLODA, N. A., 1986b. *Palynological analyses of the Upper Permian deposits of the north of the Russian Platform*. Abstract of Thesis, Kazan, 20 pp. (In Russian.)
- KOLODA, N. A., 1989. *Ventralvittatina*, a new genus of Permian striate pollen. In *Palaeontological grounds of subdivision and correlation of the Phanerozoic deposits of the European North of the USSR*. (Trudy Instituta, geologii Komi nauchnogo tsentra, Ural'skogo otdeleniya Akademii Nauk, SSSR., Syktyvkar.) *Proceedings of the Institute of Geology of the Komi Republic Scientific Centre of the Urals Branch, Academy of Sciences, USSR* 71: 60-71. (In Russian.)
- KYUNTZEL, M. K., 1965. Palynological characteristics of the Upper Permian and Lower Triassic of the basin of Vetluga and the watershed of Volga and Unzha inside the Kostroma region. In *Collection of papers on geology and hydrogeology*, issue 4: 75-80. Nedra Press, Moscow. (In Russian.)
- LOZOVSKIY, V. R., 1992. The Permian-Triassic boundary in continental series of Laurasia and its correlation with the marine scale. *International Geology Review* 34: 1008-1014.
- LUBER, A. A. & WALTZ, I. E., 1941. Atlas of microspores and pollen grains of the Palaeozoic of USSR. (Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta.) *Transactions of the all Russian Scientific Geological research Institute (VSEGEI)* 139: 108 pp. (In Russian.)
- MANGERUD, G., 1994. Palynostratigraphy of the Permian and lowermost Triassic succession, Finnmark Platform, Barents Sea. *Review of Palaeobotany and Palynology* 82: 317-349.
- MANGERUD, G. & KONIECZNY, R. M., 1993. Palynology of the Permian succession of Spitsbergen, Svalbard. *Polar Research* 12: 65-93.
- MAHESHWARI, H. K. & MEYEN, S. V., 1975. *Cladostrobus* and the systematics of Cordaitalean leaves. *Lethaia* 8: 103-123.
- MEYEN, S. V., 1973. On the relationship of the Upper Palaeozoic saccate miospores of the USSR and Indian part of Gondwana. *Palaeontological Journal* 3: 108-118. (In Russian.)
- MEYEN, S. V., 1979. Relation of Angara and Gondwana floras; a century of controversies. In *Fourth International Gondwana Symposium; Papers (Volume I)*. *International Gondwana Symposium* 4: vol. 1, 45-50.
- MEYEN, S. V., 1981a. Some true and alleged Permian conifers of Siberia and Russian Platform and their alliance. *The Palaeobotanist* 28-29: 161-176.
- MEYEN, S. V., 1981b. *Traces of Indian grasses*. Mysl Press, Moscow, 159 pp. (In Russian.)
- MEYEN, S. V., 1982. The Carboniferous and Permian floras of Angaraland (a synthesis). *Biological Memoirs* 7: 1-109.
- MEYEN, S. V., 1987. *Fundamentals of Palaeobotany*. Chapman and Hall, London and New York, 432 pp.
- MEYEN, S. V., 1992. Geography of Macroevolution in Higher Plants. *Soviet Science Review G. Geology* 1, Harwood Academic Publishers, 39-70.
- MOLIN, V. A. & KOLODA, N. A., 1972. *Upper Permian spore-pollen assemblages of North of the Russian Platform*. Nauka Press, Leningrad, 100 pp. (In Russian.)
- MOLIN, V. A. & MURAVYOVA, M. I., 1970. Palynological characteristics of the Tatarian in the basin of Mezen. In *The Palaeozoic fauna and flora from the north-east of the European part of the USSR*. Nauka Press, Leningrad, 50-61. (In Russian.)
- NASSICHUK, W. W., 1995. Permian ammonoids in the Arctic regions of the world. In *The Permian of Northern Pangea. Volume 1: Paleogeography, Paleoclimates, Stratigraphy*, P. A. Scholte, T. M. Peryt & D. S. Ulmer-Scholle, eds, Springer-Verlag, Berlin, 210-235.
- OSBORN, J. M. & TAYLOR, T. M., 1994. 7. Comparative ultrastructure of fossil gymnosperm pollen and its phylogenetic implications. In *Ultrastructure of fossil spores and pollen*, M. H. Kurmann & J. A. Doyle, eds, Royal Botanic Gardens, Kew, 99-121.
- OUYANG, S., 1982. Upper Permian and Lower Triassic palynomorphs from eastern Yunnan, China. *Canadian Journal of Earth Sciences* 19: 69-80.
- PIASECKI, S., 1984. Preliminary palynostratigraphy of the Permian-Lower Triassic sediments in the Jameson Land and Scoresby Land, East Greenland. *Bulletin of the Geological Survey of Denmark* 32: 139-144.
- PANT, D. D. & NAUTIYAL, D. D., 1960. Some seeds and sporangia of *Glossopteris* flora from Raniganj coalfield, India. *Palaeontographica, Abt. C* 107: 41-64.
- PLOTNIKOV, M. A., 1964. *The stratigraphy and lithology of the Upper Permian (Tatarian) of the Lower Mezen and Vashka regions*. Nauka Press, Moscow, Leningrad, 92 pp. (In Russian.)

- PLOTNIKOV, M. A. & MOLIN, V. A., 1969. *The Upper Permian and Lower Triassic of Western Fore-Timan*. Nauka Press, Leningrad, 107 pp. (In Russian.)
- SAMOILOVICH, S. R., 1953. Pollen and spores from the Permian deposits of the Cherdyn and Aktyubinsk Cis-Urals. In *Palaeobotanical collection*. (Vsesoiuznyi nauchno-issledovatel'skii geologo-razvedochnyi institut, Trudy, Leningrad, novaya seriya.) *Proceedings of the the All-Union Oil Scientific Research and Geological Prospecting Institute (VNIGRI)*, new series, 75: 5-57. (In Russian.)
- SCHEURING, B. W., 1974. 'Protosaccate' Strukturen, ein weit verbreitetes Pollenmerkmal zur frühen und mittleren Gymnospermenzeit. *Geologisch-paläontologische Mitteilungen Innsbruck* 4: 1-30.
- SEDOVA, M. A., 1956. [Striatopodocarpites, Striatoabietes, Striatopiceites, Striatopinites.] In *Materials of palaeontology. New families and genera*. (Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta.) *Transactions of the all Russian Scientific Geological research Institute (VSEGEI)*, new series, 12: 246-249, 351. (In Russian.)
- SIVERTSEVA, I. A., 1966a. On the Permian vegetation of the Soviet Union. In *On the methods of the palaeopalynological studies. Materials for the 2nd International Palynological conference*. Leningrad, 105-117. (In Russian.)
- SIVERTSEVA, I. A., 1966b. Permian miospore assemblages of the USSR. In *Palaeopalynology Volume II*. (Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta.) *Transactions of the all Russian Scientific Geological research Institute (VSEGEI)*, new series, 141: 100-120. (In Russian.)
- STANTCHNIKOVA, M. S., 1980. Pollen of *Vinitina* Luber ex Wilson and its significance for the Permian stratigraphy. In *Microphytofossils in oil geology (collection of works)*. Leningrad, 79-95. (In Russian.)
- STIDD, B. M. & HALL, J. W., 1970. The reproductive organs of *Callistophyton*. *American Journal of Botany* 57: 757-758.
- STROK, N. I., 1987. Late-Permian lakes of the Moscow syncline. In *The history of lakes of the Upper Palaeozoic and Lower Mesozoic*, G. G. Martinson & I. J. Neustrueva, eds, Nauka Press, Leningrad, 128-139. (In Russian.)
- TOWNROW, J. A., 1960. The Peltaspermaeaceae, a pteridosperm family of Permian and Triassic age. *Palaeontology* 3: 333-361.
- TUZHKOVA, V. I., 1985. *Miospores and stratigraphy of the reference sections of Triassic of the Urals. Lower Triassic, uppermost Permian*. (Akademia Nauk SSSR, Ural'skii nauchnyi tsentr, Sverdlovsk.) Academy of Sciences, USSR, Urals Scientific Centre, Sverdlovsk (Ekaterinburg), 232 pp. (In Russian.)
- TVERDOKHILEBOV, V. P., 1987. Late Permian lacustrine-alluvial landscapes of the southern Uralian Foreland. In *The history of lakes of the Upper Palaeozoic and Lower Mesozoic*, G. G. Martinson & I. J. Neustrueva, eds, Nauka Press, Leningrad, 149-157. (In Russian.)
- UTTING, J., 1989. Preliminary palynological zonation of surface and subsurface sections of Carboniferous, Permian and lowest Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago. In *Current Research, Part G. Geological Survey of Canada*, Paper 89-1 G, 233-240.
- UTTING, J., 1994. Palynostratigraphy of Permian and Lower Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin* 478: 107 pp.
- UTTING, J. & PIASECKI, S., 1995. Palynology of the Permian of northern continents; a review. In *The Permian of Northern Pangea. Volume 1: Paleogeography, Paleoclimates, Stratigraphy*, P. A. Scholle, T. M. Peryt & D. S. Ulmer-Scholle, eds, Springer-Verlag, Berlin, 236-261.
- UTTING, J., ESAULOVA, N. K., SILANTIEV, V. V. & MAKAROVA, O. V., 1997. Late Permian palynomorph assemblages from the Ufimian and Kazanian type sequences in Russia, and comparison with Roadian and Wordian assemblages from the Canadian Arctic. *Canadian Journal of Earth Sciences* 34: 1-16.
- VARYUKHINA, L. M., 1971. *Spores and pollen grains of the red colored and coal-bearing deposits of the Permian and Triassic of the north-east of the European part of the USSR*. Nauka Press, Leningrad, 159 pp. (In Russian.)
- VARYUKHINA, L. M., KANEV, G. P., KOLODA, N. A., MOLIN, V. A. & FEFILOVA, L. A., 1981. *Correlation of the Permian of varied facies in northern European USSR*. Nauka Press, Leningrad, 160 pp. (In Russian.)
- VIRBITSKAS, A. B., 1983. Miospores. In *Palaeontological atlas of the Permian deposits of the Pechora coal basin*, S. V. Meyen, V. A. Molin, A. B. Virbitskas, L. M. Varyukhina, N. V. Kalashnikov, S. K. Pukhonto, L. A. Fefilova, A. Gusko & G. P. Kanev, eds, Nauka, Leningrad, 92-202. (In Russian.)
- VISSCHER, H., 1971. The Permian and Triassic of Kingseout Outlier, Ireland. A palynological investigation related to regional stratigraphical problems in the Permian and Triassic of Western Europe. *Geological Survey of Ireland, Special Paper* No. 1: 114 pp.
- VISSCHER, H., 1973. The Upper Permian of Western Europe—a palynological approach to chronostratigraphy. In *The Permian and Triassic Systems and their mutual boundary*, A. Logan & L. V. Hills, eds, *Canadian Society of Petroleum Geologists* (Memoir 2), Calgary, Alberta, 200-219.
- WILSON, L. R., 1962. Permian plant microfossils from the Flowcrop Formation, Greer County, Oklahoma. *Oklahoma Geological Survey, Circular* 49: 50 pp.
- YAROSHENKO, O. P., 1990. Miospore complexes and the age of tuffaceous sedimentary strata of the Tunguska Basin. In *Palaeofloristics and stratigraphy of Phanerozoic* 2, Moscow, 44-84. (In Russian.)

- YAROSHENKO, O. P., GOLUBEVA, L. P., & KALANTAR, I. Z., 1991. Miospores and stratigraphy of Lower Triassic of Pechorskaya Synclise. *Transactions of the Geological Institute of the Academy of Sciences of the USSR* 470: 135 pp. (In Russian.)
- ZAUER, V. V., 1954. Fossil species of *Cedrus* and their significance for the stratigraphy of continental deposits. In *Materials on palynology and stratigraphy. Collection of papers*. Gosgeoltekhizdat Press, Moscow, 10-85. (In Russian.)
- ZAUER, V. V., 1960a. On the Upper Permian flora of the Solikamsk area (as evidenced by the palynological analysis). *Palaeontological Journal* 4: 114-124. (In Russian.)
- ZAUER, V. V., 1960b. New species of the vittatins from the Kamian Foreurs. In *New species of the ancient plants and invertebrates of the USSR, Part 1*. Gosgeoltekhizdat Press, Moscow, 73-78. (In Russian.)
- ZAUER, V. V., SALUJHA, S. K. & SAMOILOVICH, S. R., 1969. Comprehensive study on the Upper Permian miospores of the USSR and India. *Palaeontological Journal* 125-132. (In Russian.)
- ZORICHEVA, A. I. & SEDOVA, M. A., 1954. Spore-pollen assemblages of the Upper Permian deposits of some regions of north of the European part of the USSR. In *Materials on palynology and stratigraphy. Collection of papers*, Gosgeoltekhizdat Press, Moscow, 160-201. (In Russian.)